

Influence of prey distribution on the functional response of lizards

William C. Pitt and Mark E. Ritchie

Pitt, W. C. and Ritchie, M. E. 2002. Influence of prey distribution on the functional response of lizards. – *Oikos* 96: 157–163.

We experimentally examined the effect of invertebrate prey distribution on the functional response of a vertebrate predator. We predicted how predator consumption of prey would change with prey distribution using a scale-dependent foraging model. This model predicted that prey consumption rate should decrease as a fixed density of resources becomes more dispersed in space as measured by its fractal dimension. The model incorporates an explicit description of the spatial distribution of prey into classical optimal foraging theory. We tested this prediction with foraging trials involving lizards feeding on grasshoppers in experimental arenas with a single grass species as vegetation cover. We manipulated grasshopper distribution associated with this grass by manipulating the distribution of vegetation in arenas to yield different fractal dimensions. Skinks foraging in arenas with a few large clumps of vegetation (low fractal dimension) captured significantly more prey at all prey densities than skinks foraging in arenas with many small clumps but not necessarily more evenly dispersed (high fractal dimension). These results support the predictions of the spatially dependent foraging model, and show that prey dispersion can strongly modify the predator functional response.

W. C. Pitt and M. E. Ritchie, Dept of Fisheries and Wildlife, and Ecology Center, Utah State Univ., Logan, UT 84321-5210, USA (present address of WCP: UMC 5295, USDA, APHIS, WS, NWRC Predator Ecology, Utah State Univ., Logan, UT 84321-5295, USA [wcp@cc.usu.edu]).

Foraging success, or the ability of predators to find and consume prey, is of great importance in understanding population dynamics and interactions between species (Hassell 1978, Stephens and Krebs 1986). Often, predator foraging success is represented as a functional response, which is the relationship between the predation rate of a single predator and prey density (Holling 1959, Chant 1961, Real 1979, Kaiser 1983, Abrams 1990, Parajulee et al. 1994). The shape of the functional response may be influenced by predator characteristics, such as predator age, sex, or behavior (Holling 1959, Hardman and Turnbull 1974, Eveleigh and Chant 1981, Abrams 1990, Parajulee et al. 1994), prey characteristics, such as attractiveness or palatability (Holling 1959, Real 1979, Spitze 1985), or the spatial environment (MacArthur and Pianka 1966, Real 1979, Kaiser 1983, O'Neill et al. 1988), among other things. Although effects of predator and prey characteristics on func-

tional responses have been modeled and investigated extensively (Charnov et al. 1976, Hassell 1978, Stephens and Krebs 1986, Abrams 1990, With 1994), less attention has been given to the effect of prey and habitat distribution (Real 1979, Kaiser 1983, Hassell and Pacala 1990, Parajulee et al. 1994, Ryoo 1996, Maron and Harrison 1997).

The potential for the spatial environment to influence foraging success has been recognized for many years (Huffacker 1958, Pimental et al. 1963, Levins 1966, MacArthur and Pianka 1966, Real 1979, Kareiva 1987), but few general predictions have emerged. Hassell and Pacala (1990) and Kareiva (1990) reviewed discrete host-parasitoid and spatially explicit simulations of prey distribution that make implicit predictions of predation success in response to prey aggregation. Randomly searching predators or parasitoids are thought to have reduced predation rates when prey

Accepted 2 August 2001

Copyright © OIKOS 2002
ISSN 0030-1299

become aggregated, because predators spend time searching where prey are scarce or parasitoids attack individuals already parasitized (Hassell and May 1973, Murdoch and Stewart-Oaten 1989, Hassell and Pacala 1990, Ives 1992). Alternatively, selective predators that choose prey patches of different size based upon prey density have higher predation rates when prey are aggregated (Hassell 1978, Hassell and Pacala 1990, Kareiva 1990). However, prey aggregation and predation success have never been explored explicitly from a functional response perspective, where predator success is dependent on a range of prey densities, prey aggregation, prey patches of different sizes, and adaptation of predators.

Qualitative descriptions of the spatial distribution of prey and their habitats have proven difficult to standardize (Kaiser 1983, Kareiva and Wennergren 1995). Previous research has explored the effects of adding barriers to movement (Savino and Stein 1982, Kaiser 1983), placing resources in different spatial arrangements (Real 1979, Ryoo 1996), or adding structures to change landscape geometry (Hardman and Turnbull 1974, Parajulee et al. 1994). Fractal geometry provides a potentially simple, replicable method to describe the complex spatial geometry of prey distributions, such as patches of different sizes and shapes across a landscape (Wiens 1989, Avnir et al. 1998, Ritchie 1998). Fractal geometry allows the density and distribution of prey to be quantified with a simple mathematical expression. More specifically, fractal spatial distributions of prey can be described by a scaling law over a limited range of scales (Avnir et al. 1998): $P = VX^D$, where P is the number of prey in a landscape of extent X (length of one side of the observation "window"), V is a coefficient that reflects the density and aggregation of the prey in a landscape, and D is the fractal dimension. Fractal dimension describes the degree to which prey fill the landscape and the scale of resolution at which prey are aggregated. D can vary from 0 (i.e., a single point) to 3; lower fractal dimension implies less space-filling, and, for a given V , greater prey aggregation, while higher fractal dimensions imply more dispersed prey. This approach removes user bias of deciding the scale of resolution at which aggregation will be measured and allows a wide variety of spatial distributions to be explored (With 1994, Milne 1997).

Ritchie (1998) used fractal geometry to incorporate spatial complexity into classical foraging and functional response models. Recent studies suggest that many distributions in nature are fractal over ecologically relevant ranges of scales (Mandelbrot 1982, Milne 1992, 1997). More specifically, the model (Ritchie 1998) predicts how predator consumption rate should change over different prey distributions and when predators become limited in consumption by handling time at high prey densities (i.e., a Type II functional response; Solomon 1949, Holling 1959). Ritchie's (1998) model

recasts optimal foraging theory with explicit descriptions of the spatial distribution of prey. Simple patch models and previous modifications to functional response equations do not allow predictions of functional response or complex habitats (e.g., patches of different sizes and shapes). Although optimal foraging theory allows for qualitative predictions that are in agreement with this model, Ritchie's approach provides a method to incorporate nonlinear relationships between prey consumption and energy expenditure, prey patches of different sizes, and quantitative predictions that can be extended to populations and communities (Ritchie and Olff 1999, Ritchie and McCullough 2001). In this model, resources are assumed to be distributed within a landscape in "patches" of different size. The predator is assumed to have a threshold patch size (length) of prey to which it will respond. Patches smaller than this size are ignored by a selective predator. However, a predator may reduce its level of acceptance as prey fills more space (Ritchie 1998). The predator searches for prey through a landscape as influenced by barriers and corridors in both horizontal and vertical directions (i.e., landscape geometry). The foraging model defines predation rate or gross resource intake rate (R) as

$$R = \frac{\frac{ekv}{F+2-Q} (m^{F+2-Q} - z^{F+2-Q})}{1 + \frac{\alpha v}{F+1-Q} (m^{F+1-Q} - z^{F+1-Q})} \quad (1)$$

where e is the resource content per unit volume, v is the prey density, F is the fractal dimension of the landscape (i.e., the shape of the landscape), Q is the fractal dimension of the resource, m is the length of the largest resource patch, z is the predator's foraging scale (i.e., grain size or scale of resolution), and k and α convert the forager's scale into speed and handling time, respectively.

This scale dependent model can be reformatted in the form of a Michaelis-Menten resource uptake function (Real 1979, Tilman 1982), where prey are the resource:

$$R = \frac{vC_{\max}}{k_{1/2} + v} \quad (2)$$

This representation predicts how C_{\max} and $k_{1/2}$ change with changing prey distribution (Q) for a given prey density, V . C_{\max} is the asymptote, the maximum rate of prey consumption by a predator, and $k_{1/2}$ is the half saturation constant, the prey density at which the predator consumption rate is half of the maximum consumption rate:

$$C_{\max} = \frac{\frac{ek}{F+2-Q} (m^{F+2-Q} - z^{F+2-Q})}{\frac{\alpha}{F+1-Q} (m^{F+1-Q} - z^{F+1-Q})} \quad (3)$$

$$k_{1/2} = \frac{1}{\frac{\alpha}{F+1-Q} (m^{F+1-Q} - z^{F+1-Q})} \quad (4)$$

We tested the predictions of this model to explore general and repeatable effects of the spatial complexity of prey distribution on predator functional responses. Specifically, we were interested in using this model to predict how predation rates change with Q , the fractal dimension of the spatial distribution of prey (see Appendix). Under realistic conditions, C_{\max} should decrease with greater Q (e.g., prey more dispersed) and the half saturation constant should increase with greater Q (see Appendix). Thus, as prey fill more space in the environment but not necessarily more dispersed, the predation rate should decrease over all prey densities. This result would be expected because as prey patches are broken into smaller pieces, the encounter rate of larger, more profitable prey patches is reduced, thereby reducing prey capture rates (Ritchie and Olff 1999). This leads to increased $k_{1/2}$ because the time to find prey increases (Ritchie 1998). Increasing Q therefore also increases the mean handling time because more time is spent handling patches relative to their size, thereby reducing C_{\max} (Parajulee et al. 1994, Ryoo 1996, Ritchie 1998).

We tested these predictions in field experimental trials with lizards, prairie skinks (*Eumeces septentrionalis*), feeding on one of their principal prey species, the red-legged grasshopper *Melanoplus femurrubrum* (Orthoptera: Acrididae). Trials were performed in 1-m² arenas in which we manipulated the distribution of vegetative cover to achieve various fractal dimensions and thus different grasshopper distributions. At greater vegetation fractal dimensions, we expected the distribution of grasshoppers to become more dispersed, and we expected lizards to consume grasshoppers less rapidly and exhibit both a lower C_{\max} and greater $k_{1/2}$.

Materials and methods

We determined functional responses of prairie skinks feeding on red-legged grasshoppers in 1-m² arenas with established vegetation. Prairie skinks inhabit tallgrass prairie in the mid-continental U.S. (Conant 1975, Holechek et al. 1989) and commonly prey on grasshoppers and other arthropods in Minnesota (Breckenridge 1943). We collected 26 adult male skinks (mass \bar{x} = 6.26 g, SD = 1.32) from nearby fields. The skinks were held in captivity in a large (75.7 l) shaded terrarium at ambient environmental conditions with water provided ad libitum. Lizards were kept without food for up to 12 h before feeding trials. Preferred food items (i.e., Orthoptera, Lepidoptera larvac, Homoptera, Coleoptera, and Arachnids) were collected from fields using a sweep net and placed in the terrarium daily (Breckenridge 1943).

To generate arenas with different prey distributions, we stocked various densities of grasshoppers in 12 window screen arenas (1 m × 1 m × 1 m), which had been established as monocultures of big bluestem (*Andropogon gerardi*) in 1990. Grasshoppers were stocked in these arenas during experiments in 1990 and 1991, and 2–3 grasshoppers per arena persisted for > 30 d (M. E. Ritchie unpubl.). We pulled clumps of big bluestem from different plots to generate a gradient of fractal dimensions across the 12 arenas, while maintaining similar total cover of big bluestem between arenas. Thus, vegetation distribution ranged from a few large clumps (i.e., low fractal dimension) to many small clumps (i.e., high fractal dimension) of big bluestem. We removed any large insects (> 10 mg) by hand from each arena prior to stocking.

We computed the fractal dimension of the basal area of green vegetation in each arena with the standard box counting method (Milne 1991, 1997). We took a photograph from 2 m above each plot and generated a binary digitized image of the distribution of the basal area of grass in each plot. We counted the number of cells or boxes at least 50% filled by grass within a grid overlaying each image. We made these counts with four different box sizes (4, 8, 12, and 16 cm), which bracket skink body length. We then fit a regression line between the box length and the number of full boxes (both logarithmically transformed). The absolute value of the slope of the regression line estimates a vegetative fractal dimension (Q) of resource distribution (Fig. 1). The total cover of green vegetation in the landscape was also computed from these digitized images.

Although we did not directly manipulate the distribution of prey, removing vegetation altered where prey would be located, thus influencing Q , fractal dimension of the prey distribution. All areas in the arena could be used by the predator while searching for prey, thus yielding a landscape dimension of $F = 2$.

We measured a functional response curve for each of these 12 arenas. Each feeding trial consisted of placing a single skink in an arena with either 1, 2, 3, 4, 5, 8, 10, 15, or 20 grasshoppers from 10.00 to 14.00 on warm (> 20°C), sunny days. We collected grasshoppers (individual mass \bar{x} = 0.374 g, SD = 0.076, n = 50) daily using muslin sweep nets prior to experiments and placed uninjured individuals directly in arenas. We randomly selected skinks from the terrarium for each trial and placed them into arenas approximately 10 min after the grasshoppers had been added. After each trial, we removed skinks and any remaining grasshoppers. Grasshoppers not recovered were considered consumed by the skink. In 10 additional arenas, we stocked grasshoppers at a range of densities (1–20 per arena) without skinks. During a 4-h trial, only one grasshopper could not be found and none were found dead. If skinks escaped from the arenas, the trial was not included in the analysis. Each of the 12 arenas was

subjected to 25 trials, three for each grasshopper density from 1 to 10 and two for grasshopper densities of 15 and 20, for a total of 296 trials (not including four trials when skinks escaped). Skinks may be able to ingest 3–4 grasshoppers during the trial period (Breck-enridge 1943).

We analyzed skink functional responses for each arena using non-linear least squares regression (Number Cruncher Statistical System 97, J. Hintze, Kaysville, Utah). We fit the Michaelis-Menten response curve (Real 1979), $B_0X/(B_1 + X)$, to the cumulative number of grasshoppers eaten by skinks divided by the number of trials at a given grasshopper density for each arena. In this case, X is the grasshopper stocking density, and B_0 and B_1 are regression coefficients. This approach allowed us to compare non-transformed asymptotes (B_0) and half saturation constants (B_1) among arenas (Livdahl and Stiven 1983) and to estimate error terms for each. We then compared the relationship between vegetation fractal dimension and area (independent variables) of each arena against the asymptote and half saturation constants (dependent variables) for each arena using multiple linear regression analysis (Zar 1999). The relationship between vegetative cover and vegetation fractal dimension was tested using a simple regression.

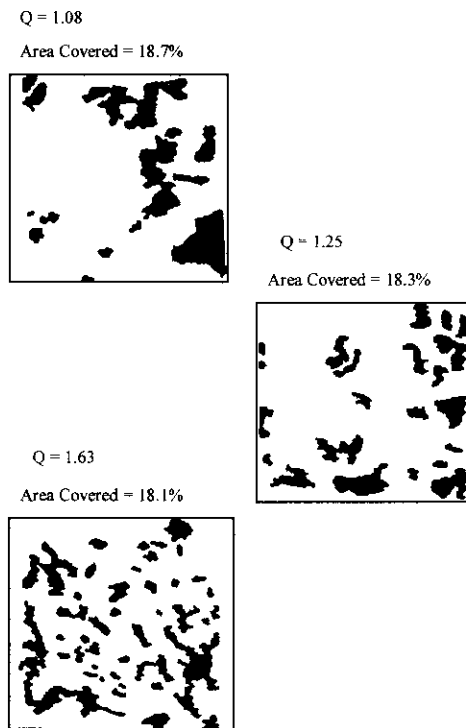


Fig. 1. Examples of digitized images of grass clumps in experimental landscapes. Area is the percent of the landscape filled by grass clumps. The vegetation fractal dimension (Q) is approximated by the absolute value of the slope of the regression line of the box count method.

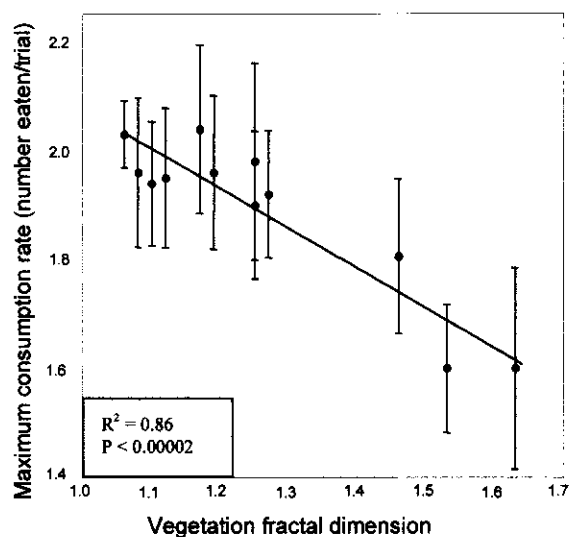


Fig. 2. Functional response curve asymptotes (C_{max} in equations) as a function of resource fractal dimension for 12 arenas ($t = -23.07$, 11 df, $p < 0.0001$). Error bars represent the 95% confidence intervals for the asymptote from the nonlinear least squares regression.

Results

Manipulated vegetation in arenas yielded fractal dimensions ranging from 1.06 to 1.63. Relationships between log cell count versus log cell length were all highly significant (all $R^2 > 0.98$, $p < 0.01$) and linear over the range of scales we explored. Vegetation cover in the 12 arenas ranged from 1290 to 2510 cm^2 but was not significantly correlated with vegetation fractal dimension (11 df, $p = 0.11$).

Grasshopper distributions also virtually matched vegetation distributions, as following each trial, we noted the location of grasshoppers prior to retrieval of the grasshoppers from the arena. Grasshoppers were found in vegetation more than 90% of the time.

The nonlinear functional response curves fit mean cumulative capture rates versus trial density well (all $R^2 > 0.58$). Increased fractal dimension of the vegetation was associated with lower asymptotes and significantly greater half saturation constants (Figs 2, 3). More specifically, skinks foraging in arenas with a few large clumps (low fractal dimension) of grass captured more prey over all prey densities than skinks foraging in arenas with many small clumps. The vegetation cover was not significantly related to estimates of asymptotes or half saturation constants (asymptote $t = -0.31$, 11 df, $p = 0.761$, half saturation constant $t = 0.41$, 11 df, $p = 0.694$). Thus, functional response shapes were strongly correlated with the spatial distribution, and not the amount of vegetation, in the arenas.

Discussion

This experiment demonstrated that prey distribution affects predator consumption rate. Prey consumption rate increased with increasing aggregation of vegetation (and presumably prey) rather than the amount of vegetation present. These results suggest that prey distribution may be critical in determining predator consumption rate in spatially heterogeneous habitats and lends support for the use of a scale-dependent foraging model (Ritchie 1998) to describe foraging behavior in spatially complex habitats.

Although spatial distributions are rarely self-similar over large scales (Avnir et al. 1998), fractals are useful to describe landscape geometry and resource distributions over ecologically relevant scales. Even if distributions are not purely fractal, fractal geometry often describes the relative abundance of small versus large patches and thus the aggregated to dispersed spatial pattern of the distribution.

Another explanation for the resulting changes in functional responses is the change in the thermal environment as vegetation became more clumped. With more open space, lizards could have achieved higher body temperatures, hence becoming more active and feeding faster. However, total vegetation cover was not correlated with consumption or fractal dimension of the vegetation so this hypothesis is unlikely to explain our results.

Our results are consistent with previous experimental tests of the influence of prey distributions on half saturation constants, that is, shifting the prey distributions from aggregated to uniform resulted in functional response curves with greater half saturation

constants (Alebeck et al. 1996a, Ryoo 1996). However, Real (1979) showed that for mice feeding on seeds, the half saturation constant decreased with more dispersed seed distributions (i.e., Q increases). Real (1979) attributed this pattern to increased learning by the predator when seeds were dispersed. Our short trial period and random selection of skinks for each trial probably meant that skinks were naïve during trials.

The same previous experimental tests have yielded mixed results in regard to the influence of prey distributions on maximum consumption rate (C_{max}). Real (1979) reported results similar to ours, that is, shifting the resource distributions from aggregated to dispersed resulted in functional response curves with lower C_{max} . However, Alebeck et al. (1996a) found that for a parasitoid wasp feeding on beetle eggs, more dispersed egg distributions yielded no change in C_{max} . This result was most likely due to females being limited in the number of eggs available rather than a function of the time spent ovipositing, because the maximum number of hosts parasitized approximated the total number of eggs available (Alebeck et al. 1996b). Ryoo (1996) showed that for mites foraging on mite egg masses, shifting the distribution of egg masses from aggregated to uniform resulted in functional response curves with greater C_{max} . This pattern reflected greater handling time, estimated from fitting experimental data to Rogers' (1972) random predator equation, when prey dispersion changed from an aggregated to a uniform pattern. Ryoo (1996) attributed greater handling time to decreased travel time between patches. Less travel time between patches leads to reduced selectivity and less time spent in a patch. Nonetheless, congruence or the lack thereof between these studies and predictions of Ritchie's (1998) model are dependent on whether C_{max} is determined by satiation (e.g., Alebeck et al. 1996b) or saturation (e.g., pursuit and handling time), the magnitude of the forager's scale (z) compared to the manipulation, and adaptive responses (Real 1979, Ryoo 1996). Adaptive responses are changes in predator searching based on past experiences with prey distributions. The adaptive responses of mice (Real 1979) and mites (Ryoo 1996) violate the assumption of our application of the scale-dependent model that foraging scale is fixed (Ritchie 1998). Because skinks were likely naïve in our trials, our experiment reduced the possibility of an adaptive response by skinks to vegetation and grasshopper distributions.

Prey aggregation has long been implicated as a stabilizing influence on predator-prey dynamics, because randomly searching predators are thought to have reduced predation rates as prey become aggregated (Hassell and May 1973, Murdoch and Stewart-Oaten 1989, Hassell and Pacala 1990, Ives 1992). However, if predators do not search randomly but select

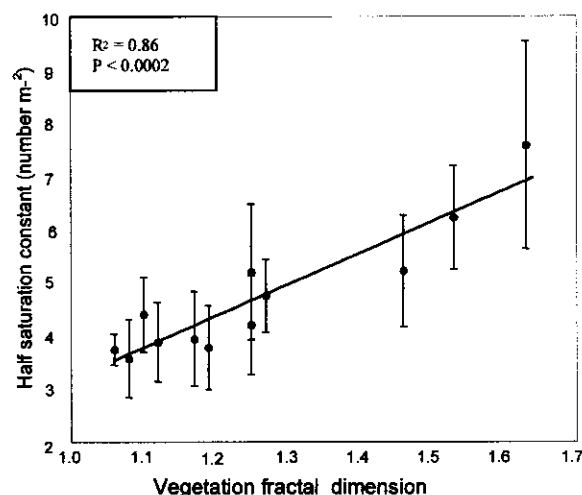


Fig. 3. Functional response curve half saturation constants as a function of resource fractal dimension for 12 arenas ($t = 7.71$, 11 df, $p < 0.0001$). Error bars represent the 95% confidence intervals for the half saturation from the nonlinear least squares regression.

patches based on prey density, predation rates increase with prey aggregation (Hassell 1978, Hassell and Pacala 1990). The lizards in our experiment responded in the latter fashion, but we can only speculate on the mechanism of such selection. As vegetation becomes more dispersed (i.e., Q increases), lizards may search many patches that do not contain prey, thereby increasing the half saturation constant. The decrease in C_{max} may be the result of an increase in the edge to area ratio of individual patches as vegetation becomes less aggregated, creating longer handling times per patch relative to the return in prey capture for lizards searching along the edge of vegetation. However, more detailed experimental work is needed to explore these mechanisms.

Our experiment supported the qualitative predictions of a scale-dependent functional response model (Ritchie 1998), but further work is warranted to determine if this model can be applied generally. Future experimental tests would be most useful if they vary prey distribution and landscape geometry (i.e., the shape and barrier structure of the arena) independently. Kaiser (1983) showed that for mites preying on mites, altering landscape geometry by adding barriers resulted in functional response curves with lower maximum consumption rates and half saturation constants. However, these barriers also increased the aggregation of prey (Kaiser 1983). Ideally, a model system to test the predictions of the model (Ritchie 1998) would allow landscape geometry and prey distribution to be manipulated independently from each other.

In natural habitats, the fractal dimension of resources would vary naturally with the biotic and abiotic conditions present in any patch and would change as animals, environmental events, and human disturbances modify habitats. For example, the clump forming grasses used in this experiment had a distribution that varied among cages according to substrate, germination events, microhabitat differences, and previous disturbances. Thus, the model results may be extended to natural population dynamics. Predators could consume more aggregated prey than dispersed prey and increased consumption rate may result in predator versus resource limited prey population dynamics or in an increase in the rate that energy moves through the food chain. However, caution should be used when applying these results to a community because the degree of aggregation is dependent on the scale of the forager and the same landscape may yield different distributions depending on the forager scale.

Acknowledgements – Our sincere gratitude is extended to the National Science Foundation (DEB-9411972) and the Ecology Center, Utah State Univ., for providing financial support. We are indebted to Gary Belovsky, Ted Evans, Russ Mason, Fred Provenza, Martyn Caldwell, Sue Durham and Mark McClure for providing editorial suggestions and statistical advice.

References

- Abrams, P. A. 1990. The effects of adaptive behavior on the type-2 functional response. *Ecology* 71: 877–885.
- Alebeck, F. A. N., van. Bezemer, T. M., Huis, A. van and Lenteren, J. C. van 1996a. The functional response of *Uscana lariophaga* under different egg distributions of its host *Callosobruchus maculatus*. *Entomol. Exp. Appl.* 81: 227–233.
- Alebeck, F. A. N., van. Koning, K., Korte, E. A. P. de and Huis, A. van 1996b. Egg-limited functional response of *Uscana lariophaga*, egg parasitoid of bruchid beetle pests in stored cowpea. – *Entomol. Exp. Appl.* 81: 215–225.
- Avnir, D., Biham, O., Lidar, D. and Malcai, O. 1998. Is the geometry of nature fractal? *Science* 279: 39–40.
- Breckenridge, W. J. 1943. The life history of the black-banded skink *Eumeces septentrionalis septentrionalis* (Baird). *Am. Midl. Nat.* 29: 591–606.
- Chant, D. A. 1961. The effect of prey density on prey consumption and oviposition in adults of *Typhlodromus* (*T.*) *occidentalis* Nesbitt (Acarina: Phytoseiidae) in the laboratory. – *Can. J. Zool.* 39: 311–315.
- Charnov, E. L., Orians, G. H. and Hyatt, K. 1976. Ecological implications of resource depression. *Am. Nat.* 110: 247–259.
- Conant, R. 1975. A field guide to reptiles and amphibians of eastern and central North America. – Houghton Mifflin Company, Boston, MA.
- Eveleigh, E. S. and Chant, D. A. 1981. Experimental studies on acarine predator-prey interactions: the numerical response of immature and adult predators (Acarina: Phytoseiidae). – *Can. J. Zool.* 59: 1407–1418.
- Hardman, J. M. and Turnbull, A. L. 1974. The interaction of spatial heterogeneity, predator competition and the functional response to prey density in a laboratory system of wolf spiders (Araneae: Lycosidae) and fruit flies (Diptera: Drosophilidae). – *J. Anim. Ecol.* 43: 155–171.
- Hassell, M. P. 1978. The dynamics of arthropod predator-prey systems. – Princeton Univ. Press.
- Hassell, M. P. and May, R. M. 1973. Stability in insect host-parasite models. *J. Anim. Ecol.* 42: 693–736.
- Hassell, M. P. and Pacala, S. W. 1990. Heterogeneity and the dynamics of host-parasitoid interactions. *Philos. Trans. R. Soc. Lond. B* 330: 203–220.
- Holechek, J. L., Pieper, R. D. and Herbel, C. H. 1989. Range management. Prentice-Hall.
- Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of European pine sawfly. *Can. Entomol.* 91: 293–320.
- Huffacker, C. B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. – *Hilgardia* 27: 343–383.
- Ives, A. R. 1992. Continuous models of host-parasitoid interactions. *Am. Nat.* 140: 1–29.
- Kaiser, H. 1983. Small scale spatial heterogeneity influences predation success in an unexpected way: model experiments on the functional response of predatory mites (Acarina). – *Oecologia* 56: 249–256.
- Kareiva, P. 1987. Habitat fragmentation and the stability of predator-prey interactions. – *Nature* 326: 388–390.
- Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. *Philos. Trans. R. Soc. Lond. B* 330: 175–190.
- Kareiva, P. and Wennergren, U. 1995. Connecting landscape patterns to ecosystem and population processes. – *Nature* 373: 299–302.
- Levins, R. 1966. The strategy of model building in population biology. *Am. Sci.* 54: 421–431.
- Livdahl, T. P. and Stiven, A. E. 1983. Statistical difficulties in the analysis of predator functional response data. – *Can. Entomol.* 115: 1365–1370.
- MacArthur, R. H. and Pianka, E. P. 1966. On optimal use of a patchy environment. – *Am. Nat.* 100: 603–609.

- Mandelbrot, B. B. 1982. The fractal geometry of nature. W.H. Freeman.
- Maron, J. L. and Harrison, S. 1997. Spatial pattern formation in an insect host-parasitoid system. – *Science* 278: 1619–1621.
- Milne, B. T. 1991. Lessons from applying fractal models to landscape patterns. In: Turner, M. G. and Gardner, R. H. (eds). *Quantitative methods in landscape ecology*. Springer-Verlag, pp. 199–235.
- Milne, B. T. 1992. Spatial aggregation and neutral models in fractal landscapes. – *Am. Nat.* 139: 32–57.
- Milne, B. T. 1997. Applications of fractal geometry in wildlife biology. – In: Bissonette, J. A. (ed.). *Wildlife and landscape ecology: effects of pattern and scale*. Springer-Verlag, pp. 32–69.
- Murdoch, W. W. and Stewart-Oaten, A. 1989. Aggregation by parasitoids and predators: effects on equilibrium and stability. – *Am. Nat.* 134: 288–310.
- O'Neill, R. V., Milne, B. T., Turner, M. G. and Gardner, R. H. 1988. Resource utilization scales and landscape pattern. – *Landscape Ecol.* 2: 63–69.
- Parajulee, M. N., Phillips, T. W. and Hogg, D. B. 1994. Functional response of *Lyctocoris campestris* (F.) adults: effects of predator sex, prey species, and experimental habitat. *Biol. Control* 4: 80–87.
- Pimental, D., Nigel, W. and Madden, J. 1963. Space-time structure of the environment and the survival of host-parasite systems. – *Am. Nat.* 97: 141–166.
- Real, L. A. 1979. Ecological determinants of functional response. *Ecology* 60: 481–485.
- Ritchie, M. E. 1998. Scale-dependent foraging and patch choice in fractal environments. *Evol. Ecol.* 12: 309–330.
- Ritchie, M. E. and Olff, H. 1999. Spatial scaling laws yield a synthetic theory of biodiversity. – *Nature* 400: 557–560.
- Ritchie, M. E. and McCullough, D. R. 2001. Spatially structured ungulate population dynamics: causes and consequences in a scaling context. – In: Merrill, E. and Irwin, L. L. (eds). *Ungulate ecology and management: integrating across spatial scales*. In press.
- Rogers, D. J. 1972. Random search and insect population models. – *J. Anim. Ecol.* 41: 369–383.
- Ryoo, M. I. 1996. Influence of the spatial distribution pattern of prey among patches and spatial coincidence on the functional and numerical response of *Phytoseiulus persimilis* (Acarina, Phytoseiidae). *J. Appl. Entomol.* 120: 187–192.
- Savino, J. F. and Stein, R. M. 1982. Predator-prey interactions between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Trans. Am. Fish. Soc.* 111: 255–266.
- Solomon, M. E. 1949. The natural control of animal populations. – *J. Anim. Ecol.* 18: 1–32.
- Spitze, K. 1985. Functional response of an ambush predator: *Chaoborus americanus* predation on *Daphnia pulex*. – *Ecology* 66: 938–949.
- Stephens, D. W. and Krebs, J. R. 1986. *Foraging theory*. – Princeton Univ. Press.
- Tilman, D. 1982. *Resource competition and community structure*. – Princeton Univ. Press.
- Wiens, J. A. 1989. Spatial scaling in ecology. – *Funct. Ecol.* 3: 383–397.
- With, K. A. 1994. Ontogenetic shifts in how grasshoppers interact with landscape structure: an analysis of movement patterns. *Funct. Ecol.* 8: 477–485.
- Zar, J. H. 1999. *Biostatistical analysis*. Prentice-Hall.

Appendix

To determine how the asymptote and half saturation constant change with changing Q , we determined the sign of the derivatives with respect to Q .

Ritchie (1998) showed that for an optimally foraging predator, $m > z$ by definition, thus we can substitute Θz for m and simplify the asymptote equation before computing the derivative:

$$C_{\max} = \frac{ek(F+1-Q)z(\theta^{F+2-Q}-1)}{\alpha(F+2-Q)(\theta^{F+1-Q}-1)}$$

The partial derivative is

$$C_{\max}(Q)' = \left(\frac{ekz}{\alpha}\right) \left(\frac{-1}{(F+2-Q)^2}\right) \left(\frac{(\theta^{F+2-Q}-1)}{(\theta^{F+1-Q}-1)}\right) + \left(\frac{zek(F+1-Q)\ln(\theta)}{\alpha(F+2-Q)}\right) \left(\frac{(\theta^{F+2-Q}-\theta^{F+1-Q})}{(\theta^{F+1-Q}-1)^2}\right)$$

$C_{\max}(Q)$ will be positive when

$$F+2-Q - \frac{(\theta^{F+1-Q})}{\ln(\theta)} > 0$$

For $F, Q < 3$, $F+2-Q < (\theta^{F+1-Q})/\ln(\theta)$ is true under all conditions, so the derivative $C_{\max}(Q)'$ is negative. Hence, as Q increases the asymptote decreases.

We simplified the half saturation equation to

$$k_{1/2} = \frac{1}{\frac{\alpha}{3-Q} (0z^{F+1-Q} - z^{F+1-Q})}$$

The partial derivative is

$$k_{1/2}(Q)' = \left(\frac{-1}{(\alpha\theta - \alpha)(z^{F+1-Q})}\right) + \left(\frac{F+1-Q}{(\alpha\theta - \alpha)(z^{F+1-Q})}\right)(\ln(z))$$

which will be positive when

$$(-1) + (F+1-Q)(\ln(z)) > 0$$

Thus, the sign of the derivative is dependent on z , where z is small ($z < 2.72$), the derivative is negative. This is the most restrictive case, when $F = Q$. However, under most conditions ($F > Q$) the derivative is likely to be positive. Since the distribution of the prey is restricted by the geometry of the landscape, F is never less than Q for foraging animals.